

EpIG-DB: A database of vascular epiphyte assemblages in the Neotropics

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Funding information

This study was financially supported by the Deutsche Forschungsgemeinschaft (DFG), funding for GML was provided (ME 5087/1-1).

Co-ordinating Editor: Meelis Pärtel

Abstract

Vascular epiphytes are a diverse and conspicuous component of biodiversity in tropical and subtropical forests. Yet, the patterns and drivers of epiphyte assemblages are poorly studied in comparison with soil-rooted plants. Current knowledge about diversity patterns of epiphytes mainly stems from local studies or floristic inventories, but this information has not yet been integrated to allow a better understanding of large-scale distribution patterns. EpIG-DB, the first database on epiphyte assemblages at the continental scale, resulted from an exhaustive compilation of published and unpublished inventory data from the Neotropics. The current version of EpIG-DB consists of 463,196 individual epiphytes from 3,005 species, which were collected from a total of 18,148 relevés (host trees and 'understory' plots). EpIG-DB reports the occurrence of 'true' epiphytes, hemiepiphytes and nomadic vines, including information on their cover, abundance, frequency and biomass. Most records (97%) correspond to sampled host trees, 76% of them aggregated in forest plots. The data is stored in a TURBOVEG database using the most up-to-date checklist of vascular epiphytes. A total of 18 additional fields were created for the standardization of associated data commonly used in epiphyte ecology (e.g. by considering different sampling methods). EpIG-DB currently covers six major biomes across the whole latitudinal range of epiphytes in the Neotropics but welcomes data globally. This novel database provides, for the first time, unique biodiversity data on epiphytes for the Neotropics and unified guidelines for future collection of epiphyte data. EpIG-DB will allow exploration of new ways to study the community ecology and biogeography of vascular epiphytes.

KEYWORDS

biodiversity, community ecology, database, forest plot, hemiepiphytes, Neotropics, nomadic vines, taxonomic diversity, vascular epiphytes, vegetation relevé



1 | INTRODUCTION

Epiphytes are plants that germinate and grow non-parasitically on other plants, mainly trees. They can be divided into non-vascular (mosses, liverworts, lichens, algae and cyanobacteria) and vascular epiphytes (e.g. orchids, bromeliads, aroids and ferns; Mendieta-Leiva, Bader, & Porada, 2020). In the case of the latter, 'true' epiphytes never establish contact with the soil, but this is different in other structurally dependent plants. Hemiepiphytes start epiphytically and later tap soil resources via aerial roots. The true nature of nomadic vines, which germinate on the ground and may (or may not) lose their initial contact with the soil, thus becoming epiphytic, to then restore (or not) contact via aerial roots is questioned and is currently under investigation (Zotz, 2013a).

Epiphytes (unless noted otherwise specifically refers to true epiphytes) fulfil important ecosystem functions related to water and nutrient cycles and biodiversity. As epiphytes have no direct contact with the soil, they often capture water and nutrients from the atmosphere (Feild & Dawson, 1998). Many epiphytes have a high capacity for water interception, storage and/or transpiration (Mendieta-Leiva et al., 2020), and they often recycle nutrients from the litter of their host tree and other epiphytes (Nadkarni & Sumera, 2004). Other functions can include maintaining and/or increasing air humidity locally (Benzing, 1998) and decreasing solar irradiation by increasing canopy cover (Cruz-Angón & Greenberg, 2005), which might positively affect the diversity of arboreal arthropod fauna (Stuntz, Simon, & Zotz, 2002). In addition, epiphytes offer food and habitat resources for many animals such as arthropods, birds or mammals (Cestari, 2009; Cruz-Angón & Greenberg, 2005; Fontoura et al., 2010).

The assembly of vascular epiphytes strongly depends on the growth of their host trees and the spatiotemporal variation of related ecological niches on each host tree (Parra, Acuña, Corcuera, & Saldaña, 2009; Taylor & Burns, 2015; Zotz & Vollrath, 2003). During host tree ontogeny, the total bark area as well as the environmental heterogeneity increases as a function of tree architecture, growth rate and crown dynamics (Einzmann, Beyschlag, Hofhansl, Wanek, & Zotz, 2014; Flores-Palacios & García-Franco, 2006; Sarmiento Cabral et al., 2015; Wagner, Mendieta-Leiva, & Zotz, 2015; Wagner & Zotz, 2020; Zotz & Vollrath, 2003). The characteristics of host individuals in combination with the vertical stratification of the forest stand may allow for an impressive number of epiphyte species to coexist in a single tree (Hietz, Winkler, Scheffknecht, & Hulber, 2012; Petter et al., 2016; Ruiz-Cordova, Toledo-Hernández, & Flores-Palacios, 2014), the record being over 200 species found on a single tree in a cloud forest in Peru (Catchpole & Kirkpatrick, 2011). Nevertheless, the lack of comparative studies makes it difficult to assess whether major drivers of local species richness are consistent across regions.

Globally, vascular epiphytes are primarily found in the tropics and subtropics, and exhibit a pronounced latitudinal diversity gradient, with their diversity peaking in the Neotropics (Gentry & Dodson, 1987; Zotz, 2016). Epiphytes contribute substantially to global species richness, accounting for ca. 9% of all vascular plant

species (Zotz, 2013b) and in some cases up to 50% of local plant species richness (Kelly, Tanner, Lughadha, & Kapos, 1994). Compared with other life forms, such as trees and lianas, vascular epiphytes show higher degrees of endemism (Cascante-Marin & Nivia-Ruiz, 2013; Freitas et al., 2016; Van der Werff & Consiglio, 2004). Nonetheless, biodiversity patterns of this hyper-diverse group are poorly known, because most efforts to understand epiphyte diversity in the Neotropics are at the level of local, idiosyncratic studies or floristic inventories.

At large spatial scales (e.g. elevational transects), the literature on biogeographic diversity patterns of epiphytes is scarce (e.g. Krömer, Acebey, Kluge, & Kessler, 2013; Krömer, Kessler, Gradstein, & Acebey, 2005; Zuleta, Benavides, López-Rios, & Duque, 2016). For example, the general notion that broad-scale gradients in epiphyte species richness are very strongly linked to moisture availability is based on just a few studies (Gentry & Dodson, 1987; Kreft, Köster, Küper, Nieder, & Barthlott, 2004; Küper, Kreft, Nieder, Köster, & Barthlott, 2004; Wester et al., 2011). Indeed, current hypotheses about macroecological patterns of epiphyte diversity are mostly based on regional or national species lists without a proper compilation of spatially explicit data, despite the wealth of local studies, for which underlying data are typically not available (Mendieta-Leiva & Zotz, 2015). In addition, the available data on vascular epiphytes are taxonomically and geographically biased, with studies mostly focused on orchids and bromeliads, and concentrated in certain regions (Zotz, 2016). A necessary step for a better understanding of the community ecology and biogeography of vascular epiphytes is to broaden our knowledge base by mobilizing and integrating existing data (on community composition, species abundance and richness) and make it available to the scientific community.

As a contribution towards this goal, we present a database infrastructure for collecting and integrating diversity data on vascular epiphyte assemblages. This will allow epiphyte ecology to move beyond local studies. We expect this effort to be both an important step in the development of epiphyte ecology but also in community ecology and biodiversity research, promoting the expansion of ecological research in the tropics by including this important biodiversity component. Moreover, in combination with detailed knowledge on the ecology and physiology of species, EpiG-DB has the potential to help us to understand the distribution of organisms and the extent of their ecological roles (e.g. contribution to the water and nutrient cycling, buffering potential, etc.), all of which will help us to better understand community and biome dynamics under current and future changes in climate and habitats.

1.1 | International consortium on epiphytic plant assemblages

The Epiphyte Inventory Group (EpiG) was formed in 2018 as a working group for collecting and analysing vascular epiphyte assemblage data. The group was established during a workshop at the University of Marburg (Germany), with the participation of 25 experts in the fields

of epiphyte ecology, database management and macroecology. The participants of the workshop represented most of the research groups working on vascular epiphytes in the Neotropics. The aims of the database consortium were (a) to create a database following international standards for integration of plant community data; (b) to establish the specific properties of a database for managing and integrating data on vascular epiphyte assemblages; (c) to discuss taxonomic issues related to data generally collected on vascular epiphytes; (d) to develop a roadmap for updating and analysing this database. These objectives were achieved by a combination of plenary discussions and parallel sessions with topic specialists, defining a set of agreement protocols that were synthesized in a document that served as a basis for this paper.

1.2 | Description of epiphyte assemblage records

We used TURBOVEG for Windows (Hennekens & Schaminee, 2001) as the reference software for digitizing data, implementing a species checklist ('epiphytes') based on a new Global Checklist of Vascular Epiphytes (Zotz, unpub., an updated version of Zotz, 2013b). In the database, the minimum sampling unit of reference is a host individual (generally a tree, thus hereafter referred to as such), which is also marked and sampled (e.g. ID, tree species, tree height, tree diameter at breast height or DBH, Appendix S1). Many times, host individuals were sampled nested within forest plots (Figure 1). Typical information for a sampled host includes the presence, surface cover, abundance, frequency or biomass of resident epiphytes. Frequently, datasets also report the absence of epiphytes from a potential host. In very few cases, the minimum sampling unit is a plot, i.e. an area in which epiphytes have been sampled without distinction of host individuals, referred to as 'understorey' plots (Krömer, Kessler, & Gradstein, 2007). In 'understorey' plots, epiphytes may be sampled until a determined height or throughout the whole canopy (sensu Moffett, 2000). In the former case, this is because epiphyte flora on shrubs and small trees in the forest understory is usually different from that on the large canopy trees (Krömer et al., 2007). Each species list sampled on a single host individual or in an 'understorey' plot corresponds to a species assemblage, called a 'relevé' in TURBOVEG. When species were sampled on host individuals nested within forest plots (Figure 1), the records were kept to the minimum sampling unit (host individual), thus allowing the user to summarize the data at larger scales when needed.

We accepted records of vascular epiphytes in the broad sense ('true' epiphytes, hemiepiphytes and nomadic vines sensu Zotz (2013a)). It is permitted to include morphospecies but vines, lianas and accidental epiphytes are excluded (Zotz, 2013a). Morphospecies are considered under the assumption that the data contributors made a conscientious effort to differentiate these as potentially different species. We are aware that in the majority of cases these morphospecies will remain unresolved but, in some cases, species names may be assigned later. Nonetheless, we consider this data necessary and important to answer several questions, for example those related to alpha diversity. Morphospecies need to include the data contributors' collection number (e.g. '*Polypodium* SB1001') or

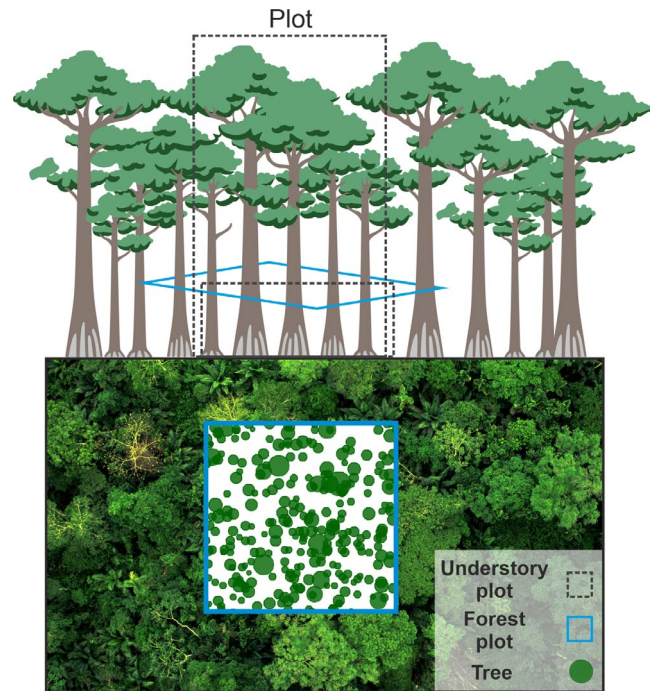


FIGURE 1 Graphical representation of the structure of epiphyte inventory data. Vascular epiphyte assemblage records in EpiG-DB 1.0 have as minimum sampling unit the entire host individual for which relevant ecological data must be collected (Appendix S1). Commonly, host individuals (mostly trees, shown as dark green circles of different sizes according to their diameter at breast height) may be sampled within a forest plot (cyan squares), thus trees are nested within forest plots. The minimum sampling unit may also be an 'understorey' plot, i.e. a determined volume where epiphytes have been sampled without distinction of the host individuals (dotted line squares), sometimes focused on the understory, thus of a certain height. Photo credit to the Department of Geoinformatics, Munich University of Applied Sciences. Forest diagram modified after Gunnar Petter

an unambiguous name assigned by the contributor. Species that are identified as 'cf.' can be kept if the record is a distinct morphospecies (removing the cf. and indicating the epithet as the species it is compared with, e.g. *Polypodium* cf. *vulgare* becomes *Polypodium vulgare*). Species that are identified as 'aff.' can be considered as a morphospecies. For example, 'vel. aff.' means: this species or related, while 'aff.' means not this species, but related, all as part of the epithet or morphospecies name (e.g. *Polypodium* aff. *vulgare* becomes *Polypodium affvulgare*). Varieties and subspecies are all considered at the species level. Juveniles that could not be determined or differentiated into morphospecies are excluded. Morphospecies are manually added to the species checklist but they can be omitted in specific data analyses.

1.3 | Data collection, harmonization and integration

We contacted the largest number of researchers working on epiphytes that we could reach and provided a protocol for importing



data into TURBOVEG, a comprehensive database management system for vegetation data (Hennekens & Schaminee, 2001). The integration was carried out using the species checklist 'epiphytes' and a predefined list of associated data ('header data' in TURBOVEG, see below). As our data protocol included specialized qualifiers for species data (e.g. biomass data) and header data (e.g. host ID), we recommended updating TURBOVEG with a specific version provided by the software developer (S. Hennekens). The data contributors were asked to upload their data to the updated version of TURBOVEG using the following steps: (a) to clean species names using taxonstand (Cayuela, Granzow-de la Cerda, Albuquerque, & Golicher, 2012) and the database of The Plant List (2013) to facilitate data import; (b) to standardize their associated data (Appendix S1); (c) to provide a metadata statement including the Author (name of the person/people who collected the data), Reference (if published), Project (if data was collected within the frame of a specific project), and Funding institution (if the project was funded; Appendix S2).

The data associated with each record ('header data') was predefined by the EpiG working group for harmonizing the individual datasets before integration. We added 18 additional fields (Appendix S1) to the header data available by default in TURBOVEG, which take into account the protocols used for sampling epiphytes (Gradstein et al., 1996; Gradstein, Nadkarni, Holz, Nöske, & Krömer, 2003; Krömer & Gradstein, 2016; Zotz & Bader, 2011). Twelve of these fields are mandatory because they provide essential information regarding sampling protocols (e.g. longitude and latitude, host DBH, and naturalness as in Bruelheide et al. (2019)). The other six optional fields may be useful for specific analyses (e.g. x and y coordinates, host height, host name, vegetation type). Header data were integrated into a single database into TURBOVEG. The data aggregated at the forest plot level were registered in the Global Index of Vegetation-Plot Databases (www.givd.org) with the ID-Number SA-00-003 and added to the sPlot consortium (www.idiv/splot.de).

1.4 | Description of the database

The current version of EpiG-DB (version 1.0; December 2019) comprises 18,148 relevés of which 17,762 represent trees and 386 represent 'understorey' plots, in which epiphytes were sampled without reference to trees. Most trees (76%) were sampled within 687 forest plots ranging from 25 to 22,500 m² (Figure 1, Appendix S3). These and the 'understorey' plots comprise the EpiG-DB plot version, which will be part of sPlot (3.0) after aggregating the information at the forest plot and not the host tree level.

The database includes 2045 identified species of vascular epiphytes and 960 morphospecies. Species are distributed within 411 genera and 60 families. The taxonomic distribution of species per family reflects the expected pattern with orchids representing most of the species richness, making up 38% of species, followed by bromeliads and aroids (768, 241, and 201 epiphyte species, respectively). These three families alone make up almost 60% of species richness. Distribution of genera across families is slightly different,

although orchids are also the most genus-rich family, comprising over 40% of genera. They are followed by polypod ferns, bromeliads and ericads. Together, these families comprise almost 60% of all genera (142, 28, 17, and 13 genera, respectively).

The organization of the EpiG-DB reflects the ecological particularities of vascular epiphytes as structurally dependent life forms with 18 new fields added to the standard TURBOVEG header data (Appendix S1). In the case of trees being nested within a forest plot, information for both the plot and host individuals is included in the relevé ID by combining the names of the plot and tree IDs. In addition, the coordinates of each tree can be provided (X and Y coordinates, Appendix S1) in combination with a tree ID and the corresponding plot ID. While the ID data is mandatory, X and Y coordinates data were provided for just 8% of all forest plots. When all trees in a forest plot were sampled, relevés may also be 'empty'. This is the case for 30% of the relevés. Alternatively, when the minimum sampling unit is an 'understorey' plot, i.e. an area where the epiphytes were sampled without distinction of hosts, the unambiguous distinction between 'understorey' plot or tree is given in the field 'plot/tree'.

Sampling of vascular epiphytes was carried out differently depending on forest type and the research aims of each field team. Thus the specification of the sampling method (Appendix S1) is provided for all relevés. The most common sampling method included a combination of tree climbing and ground observation with binoculars (56%). Ground observation with binoculars or climbing alone is used in second and third place (31% and 11%, respectively), and only a very small number of relevés were sampled using ground observation without optical devices (<1%). The assessment of the abundance is also heterogeneous in epiphyte sampling. In addition to presence/absence, which is straightforward, abundance may be quantified as the number of individuals or stands (Sanford, 1968), biomass or frequency (Appendix S1). The latter refers to the number of Johansson zones (Johansson, 1974) in which an epiphyte species was found within a single host. In EpiG-DB the majority of relevés had some measure of abundance (74%, mostly number of individuals), while presence/absence data was only recorded for 20% of trees and for all those plots where sampling was not on a tree base ('understorey' plots). To a smaller extent data represent frequency and biomass (ca. 6%).

Information on the taxonomic groups and the life forms (sensu Zotz, 2013a) sampled were included. In almost 60% of relevés all vascular plants were sampled, while in ca. 30% only angiosperms and in a 13% of relevés only selected taxa were sampled (mostly ferns, orchids and bromeliads). The majority of the relevés include all three life forms (45%, epiphytes, hemiepiphytes and nomadic vines) or a combination of epiphytes and either hemiepiphytes (20%) or nomadic vines (11%). Only a small number of relevés include a single life form (e.g. epiphytes only 16% and hemiepiphytes only 8%).

The characteristics of host individuals are well documented in EpiG-DB. For example, 92% of all trees have DBH data while 63% have height data and 85% have been identified at least to the genus level. The data on host size revealed that the DBH of the majority of the sampled trees fall between 5 cm and 30 cm with

very few large trees >100 cm DBH comprising about 2% (390 trees, Appendix S4).

Naturalness of sampling sites was provided for all relevés in all datasets and indicates that relevés are mainly distributed in natural ecosystems (66%) and to a lesser degree in anthropogenic (19%) and semi-natural (15%) ecosystems.

1.5 | Spatial and sample coverage

The first version of the database covers most of the potential latitudinal distribution of vascular epiphytes in Tropical and Subtropical America (Figure 2). We plotted all records (sampled understory plots and hosts) across a map of terrestrial world biomes for the American tropics and subtropics. We used the classification of the WWF (Olson et al., 2001), which comprises 14 terrestrial world biomes based on existing global maps of floristic or zoogeographic provinces, the world's biotic province maps and global maps of broad vegetation types, and defines 867 Ecoregions based on regional classification systems and expert opinion. Our datasets are distributed across nine countries, eight biomes and 45 WWF ecoregions out of the 234 recorded in the Neotropics (Olson et al., 2001).

To assess the climatic representativity of our data, we obtained two bioclimatic variables (mean annual temperature and annual precipitation) for all records using geographic coordinates from CHELSA (Karger et al., 2017). For matching our data with major gradients of mean annual temperature and annual precipitation we applied Whittaker's biome model (Whittaker, Levin, & Root, 1975), using the *plotbiomes* (Ricklefs, 2008, <https://github.com/valentinitnelav/plotbiomes>) and *ggplot2* (Wickham, 2016) packages. The climate range of datasets covers tropical and subtropical biomes of the Neotropics where epiphytes are generally found (Figure 3). Some datasets were located outside of designated biome areas, such as in cold and very rainy ecoregions from the tropics (e.g. the Peruvian Yungas, Eastern Cordillera real montane forests and northern Andean páramo; Figure 3).

Finally, for assessing relative sample completeness (the relationship between sample coverage and species diversity, Chao et al., 2014) across WWF Ecoregions (Olson et al., 2001), we used sampled-based rarefaction curves based on interpolation and extrapolation of species richness with the *iNext* package (Hsieh, Ma, & Chao, 2016). Species diversity refers to species richness (Hill numbers, $q = 0$, Hsieh et al., 2016). Sample coverage was calculated using frequency data and only for ecoregions with at least 100 trees sampled. Sampling completeness reveals the large variability in sampling coverage across ecoregions and points to those where more sampling effort is needed (Figure 4, Appendix S5).

In ecoregions of South America, very few of the confidence intervals overlap except at very small coverage values, implying significant differences in epiphyte diversity among ecoregions at comparable coverage; this was not the case for most ecoregions in Central America (Figure 4), where diversity seems to be comparable among most ecoregions. In certain ecoregions, undersampling was

very high (e.g. Bolivian Yungas and Cauca Valley montane forests), whereas in some other regions (e.g. Chaco, Bahia interior forests and Campos Rupestre Montane savanna) sampling seems to have reached a high degree of completeness (Figure 4).

1.6 | Further perspectives

EplG-DB consists of fine-grained data sampled at the local scale and integrated at a wide geographical spread, including many datasets with unpublished information on epiphyte abundance, which have been made available to the scientific community. Analyses of the database will be instrumental not only in answering questions related to large-scale patterns of epiphyte assemblages, but will also contribute to the understanding of plant diversity in general with a broad biogeographic and macroecological focus. EplG-DB also aims to collate vascular epiphyte inventory data across the world. The current database comprises a substantial and important amount of data and sites - from nine countries, eight biomes and 45 ecoregions in the Neotropics, and it also reveals how many ecoregions and ecosystem types are not yet accounted for (Appendix S5). This effort needs to be extended geographically and, most importantly, it needs to include data already collected which may or may not be described in grey literature and is at risk of being lost.

Future efforts in data sampling or data collection will need to consider current biases towards Central America and southeast/southern Brazil, near the Atlantic coast and towards natural habitats. The lack of data from the Caribbean and Amazonia reflects undersampling in these regions, where current data are distributed across a few locations. The inclusion of epiphyte inventory data from Africa, Asia and Oceania is planned and will need to start with the most available data, but it is unlikely that these will cover the latitudinal and climatic gradients as well as the current dataset does in the Neotropics. Therefore, datasets from tropical and subtropical regions outside of the Neotropics are highly welcome.

Vascular epiphytes as structurally dependent organisms, which grow on dynamic island-like substrates, fundamentally differ from terrestrial plants in their population and community dynamics. Further, their considerable contribution to diversity and biomass in tropical ecosystems makes them an important Neotropical diversity component. Compared with, for example trees, epiphytes are particularly vulnerable to the effects of landscape modification and climate change, particularly in montane cloud forests, because of their tight coupling with the atmosphere and structural dependency (Laube & Zotz, 2006; Zotz, Bogusch, Hietz, & Ketteler, 2010; Zotz & Hietz, 2001). Therefore, the presence of certain species may reflect a conserved state of the forest (Benzing, 1990). Predictions of the effect of climate change for mountain forests imply a decrease in atmospheric water availability (e.g. dew and mist; Feeley et al., 2011; Urrutia & Vuille, 2009), which would negatively affect epiphyte biomass and have a cascading effect in the ecosystem. Efforts in conservation will be more informed and ultimately more successful with a clear theoretical understanding of the diversity and dynamics of epiphyte assemblages.

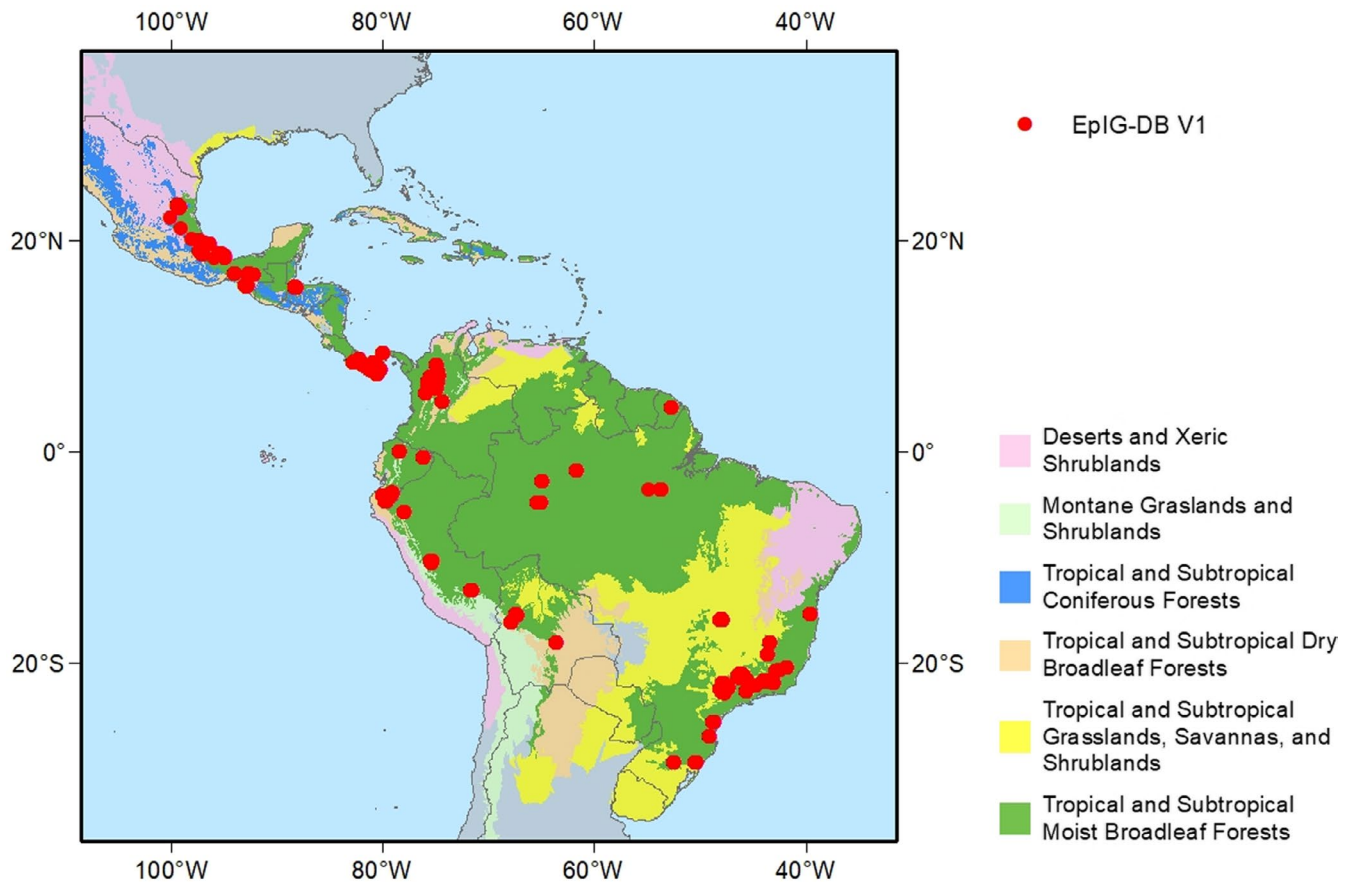


FIGURE 2 Spatial distribution of 40 datasets integrated in EpIG-DB 1.0 across the Neotropic WWF biomes

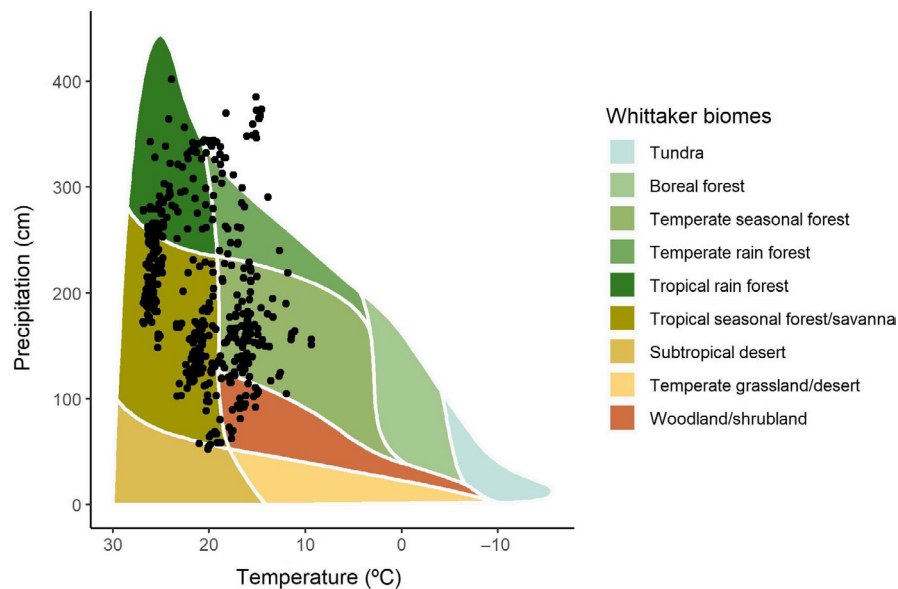


FIGURE 3 Climate envelope of EpIG-DB 1.0 data (black dots) across Whittaker biomes. The Whittaker plot shows the distribution of vegetation types as a function of mean annual temperature and precipitation

1.7 | Database consortium and data use agreements

We strongly encourage epiphyte ecologists to contribute to this database initiative. To this end, we recommend future epiphyte

inventories and database managers collect in the standardized format proposed here, including at least the following data: (a) epiphyte abundance per host individual, (b) epiphyte species, (c) host individual species, (d) host tree DBH and height, (e) host

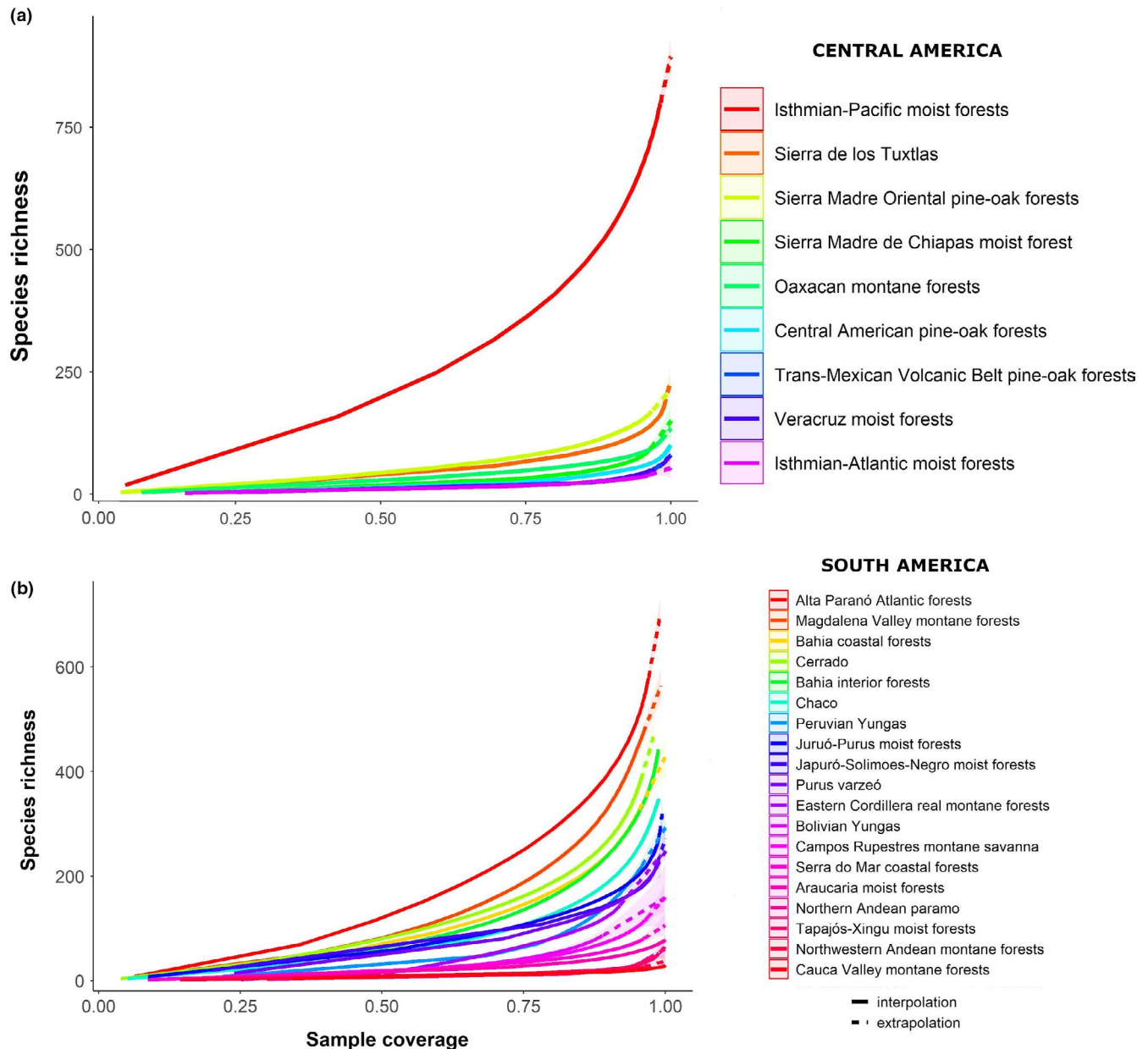


FIGURE 4 Coverage-based rarefaction (interpolation) and extrapolation plots for vascular epiphyte diversity per ecoregion and subcontinent. The curves indicate the observed (interpolated) and extrapolated species richness with respect to sample coverage (number of trees) for 28 out of the 45 ecoregions for which at least 100 entire trees were sampled. For (a) Central America there are nine ecoregions and for (b) South America 19 ecoregions. The colour gradient follows species diversity according to ecoregion and the shaded polygons represent 95% confidence intervals. Calculations are based on incidence data

coordinates, and (f) whenever sampling within forest plots to also include empty (potential) host individuals. The EpIG-DB consortium is open to any researcher willing to contribute data, especially from poorly sampled regions within the Neotropics and across the world.

For the completion of first data analyses, only database contributors can access and use the data during the first two years (until March 2022). After the embargo period, all data will be made available to any researcher upon request through a digital repository (e.g. Zenodo) that provides the option of conditional access. As the database contains

georeferenced records and information of abundance, there is a danger of misuse for the illegal collection of endangered species. We, therefore, will not allow completely open access, but researchers with a legitimate interest will be given full access by the database curators under conditions ensuring that the data will not be shared outside of academia. Regarding authorship agreements, by default, we will apply the principles stated in the sPlot rules (Bruehlheide et al., 2019) to which this database is also contributing. Any request should be done by contacting the Custodian (Glenda Mendieta-Leiva) or the Deputy Custodian (Borja Jiménez-Alfaro).



ACKNOWLEDGMENTS

We thank to Stephan Hennekens for adding new functionalities to TURBOVEG, and Gabriela García Reynaga and Leonie Hahn for helping with data standardization. We express our gratitude to those helping with data collection and to several institutions for providing funding for the respective projects, both, people and institutions are indicated in Appendix S2.

AUTHOR CONTRIBUTIONS

GML had the original idea and led the consortium from the start, while GZ provided support throughout the conception of the idea, funding application and conceptualization of the workshop. GML coordinated the workshop and together with FNR, GZ, MAT, SPB, AMB, ERM, HJRE, VGJ, PH, MVI, DAJL, MK, HK, TK, NMM, ACQ, EASM, AT, JHDW, CZ and DZ contributed to the foundation of the manuscript under the guidance of BJA. GML compiled the datasets to be included in EplG with the help of JPCE. GML and BJA led the writing together with FNR and input from GZ, and comments and suggestions by MAT, SPB, AMB, MJC, HJRE, ALG, PH, MVI, DAJL, MK, HK, TK, NMM, SRM, LP, AT, KW, FAW, JHDW and DZ. All authors (except for AT and BJA) contributed data. All authors agreed with the final manuscript.

DATA AVAILABILITY STATEMENT

The data contained in EplG will be available on request, after the embargo period, through contacting the custodian and deputy custodian for submitting a paper proposal. The EplG consortium follows the Governance and Data Property Rules of the sPlot Working Group, which are available on the sPlot website (<https://www.idiv.de/en/splot.html>). The respective data will be provided after acceptance.

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REFERENCES

- Benzing, D. H. (1990). *Vascular epiphytes. General biology and related biota*. Cambridge: Cambridge University Press.
- Benzing, D. H. (1998). Vulnerabilities of tropical forest to climate change: The significance of resident epiphytes. *Climate Change*, 39, 519–540.
- Bruehlheide, H., Dengler, J., Jiménez-Alfaro, B., Purschke, O., Hennekens, S. M., Chytrý, M., ... Zverev, A. (2019). sPlot - A new tool for global vegetation analyses. *Journal of Vegetation Science*, 30, 161–186. <https://doi.org/10.1111/jvs.12710>
- Cascante-Marin, A., & Nivia-Ruiz, A. (2013). Neotropical flowering epiphyte diversity: Local composition and geographic affinities. *Biodiversity and Conservation*, 22, 113–125. <https://doi.org/10.1007/s10531-012-0404-1>
- Catchpole, D. J., & Kirkpatrick, J. B. (2011). The outstandingly speciose epiphytic flora of a single strangler fig (*Ficus crassiuscula*) in a Peruvian montane cloud forest. In L. A. Bruijnzeel, F. N. Scatena, & L. S. Hamilton (eds.) *Tropical montane cloud forests* (pp. 142–146). Cambridge, UK: Cambridge University Press.
- Cayuela, L., Granzow-de la Cerda, I., Albuquerque, F. S., & Golicher, D. J. (2012). TAXONSTAND: An R package for species names standardisation in vegetation databases. *Methods in Ecology and Evolution*, 3, 1078–1083. <https://doi.org/10.1111/j.2041-210X.2012.00232.x>
- Cestari, C. (2009). Epiphyte plants use by birds in Brazil. *Oecologia Australis*, 13, 689–712. <https://doi.org/10.4257/oeco.2009.1304.12>
- Chao, A., Gotelli, N. J., Hsieh, T. C., Sander, E. L., Ma, K. H., Colwell, R. K., & Ellison, A. M. (2014). Rarefaction and extrapolation with Hill numbers: A framework for sampling and estimation in species diversity studies. *Ecological Monographs*, 84, 45–67. <https://doi.org/10.1890/13-0133.1>
- Cruz-Angón, A., & Greenberg, R. (2005). Are epiphytes important for birds in coffee plantations? An experimental assessment. *Journal of Applied Ecology*, 42, 150–159. <https://doi.org/10.1111/j.1365-2664.2004.00983.x>
- Einzmann, H. J. R., Beyschlag, J., Hofhansl, F., Wanek, W., & Zotz, G. (2014). Host tree phenology affects vascular epiphytes at the physiological, demographic and community level. *AoB Plants*, 7, plu073. <https://doi.org/10.1093/aobpla/plu073>
- Feeley, K. J., Silman, M. R., Bush, M. B., Farfan, W., Cabrera, K. G., Malhi, Y., ... Saatchi, S. (2011). Upslope migration of Andean trees. *Journal of Biogeography*, 38, 783–791. <https://doi.org/10.1111/j.1365-2699.2010.02444.x>
- Feild, T. S., & Dawson, T. E. (1998). Water sources used by *Didymopanax pittieri* at different life stages in a tropical cloud forest. *Ecology*, 79, 1448–1452. [https://doi.org/10.1890/0012-9658\(1998\)079\[1448:W-SUBDPJ\]2.0.CO;2](https://doi.org/10.1890/0012-9658(1998)079[1448:W-SUBDPJ]2.0.CO;2)
- Flores-Palacios, A., & García-Franco, J. G. (2006). The relationship between tree size and epiphyte species richness: Testing four different hypotheses. *Journal of Biogeography*, 33, 323–330. <https://doi.org/10.1111/j.1365-2699.2005.01382.x>
- Fontoura, T., Cazetta, E., Nascimento, W. D., Catenacci, L., De Vleeschouwer, K., & Raboy, B. (2010). Diurnal frugivores on the Bromeliaceae *Aechmea depressa* LB Sm. from Northeastern Brazil: The prominent role taken by a small forest primate. *Biota Neotropica*, 10, 351–354. <https://doi.org/10.1590/S1676-06032010000400041>
- Freitas, L., Salino, A., Neto, L. M., Elias Almeida, T., Mortara, S. R., Stehmann, J. R., ... Forzza, R. C. (2016). A comprehensive checklist of vascular epiphytes of the Atlantic Forest reveals outstanding endemic rates. *Phytokeys* 58, 65–79. <https://doi.org/10.3897/phytokeys.58.5643>
- Gentry, A. H., & Dodson, C. H. (1987). Diversity and biogeography of neotropical vascular epiphytes. *Annals of the Missouri Botanical Garden* 74, 205–233. <https://doi.org/10.2307/2399395>
- Gradstein, S. R., Hietz, P., Lücking, R., Lücking, A., Sipman, H. J. M., Vester, H., ... Gardette, E. (1996). How to sample the epiphytic diversity of tropical rain forests. *Ecotropica*, 2, 59–72.
- Gradstein, S. R., Nadkarni, N. M., Holz, I., Nöske, N., & Krömer, T. (2003). A protocol for rapid and representative sampling of vascular and non-vascular epiphyte diversity of tropical rain forests. *Selbyana*, 24, 105–111.
- Hennekens, S. M., & Schaminee, J. H. J. (2001). TURBOVEG, a comprehensive data base management system for vegetation data. *Journal of Vegetation Science*, 12, 589–591. <https://doi.org/10.2307/3237010>
- Hietz, P., Winkler, M., Scheffknecht, S., & Hulber, K. (2012). Germination of epiphytic bromeliads in forests and coffee plantations:



- Microclimate and substrate effects. *Biotropica*, 44, 197–204. <https://doi.org/10.1111/j.1744-7429.2011.00791.x>
- Hsieh, T. C., Ma, K. H., & Chao, A. (2016). iNEXT: An R package for rarefaction and extrapolation of species diversity (Hill numbers). *Methods in Ecology and Evolution*, 7, 1451–1456. <https://doi.org/10.1111/2041-210x.12613>
- Johansson, D. (1974). Ecology of vascular epiphytes in West African rain forest. *Acta Phytogeographica Suecica*, 59, 1–136.
- Karger, D. N., Conrad, O., Böhner, J., Kawohl, T., Kreft, H., Soria-Auza, R. W., ... Kessler, M. (2017). Climatologies at high resolution for the earth's land surface areas. *Scientific Data*, 4, 170122. <https://doi.org/10.1038/sdata.2017.122>
- Kelly, D. L., Tanner, E. V. J., Lughadha, E. M. N., & Kapos, V. (1994). Floristics and biogeography of a rain-forest in the Venezuelan andes. *Journal of Biogeography*, 21, 421–440. <https://doi.org/10.2307/2845760>
- Kreft, H., Köster, N., Küper, W., Nieder, J., & Barthlott, W. (2004). Diversity and biogeography of vascular epiphytes in Western Amazonia, Yasuni, Ecuador. *Journal of Biogeography*, 31, 1463–1476. <https://doi.org/10.1111/j.1365-2699.2004.01083.x>
- Krömer, T., Acebey, A., Kluge, J., & Kessler, M. (2013). Effects of altitude and climate in determining elevational plant species richness patterns: A case study from Los Tuxtlas, Mexico. *Flora - Morphology, Distribution, Functional Ecology of Plants*, 208, 197–210. <https://doi.org/10.1016/j.flora.2013.03.003>
- Krömer, T., & Gradstein, R. (2016). Vascular epiphytes. In T. H. Larsen (Ed.), *Core standardized method for rapid biological field assessment*. Arlington, VA: Conservation International.
- Krömer, T., Kessler, M., & Gradstein, S. R. (2007). Vertical stratification of vascular epiphytes in submontane and montane forest of the Bolivian Andes: The importance of the understory. *Plant Ecology*, 189, 261–278. <https://doi.org/10.1007/s11258-006-9182-8>
- Krömer, T., Kessler, M., Gradstein, S. R., & Acebey, A. (2005). Diversity patterns of vascular epiphytes along an elevational gradient in the Andes. *Journal of Biogeography*, 32, 1799–1809. <https://doi.org/10.1111/j.1365-2699.2005.01318.x>
- Küper, W., Kreft, H., Nieder, J., Köster, N., & Barthlott, W. (2004). Large-scale diversity patterns of vascular epiphytes in Neotropical montane rain forests. *Journal of Biogeography*, 31, 1477–1487. <https://doi.org/10.1111/j.1365-2699.2004.01093.x>
- Laube, S., & Zotz, G. (2006). Neither host-specific nor random: Vascular epiphytes on three tree species in a Panamanian lowland forest. *Annals of Botany*, 97, 1103–1114. <https://doi.org/10.1093/aob/mcl067>
- Mendieta-Leiva, G., Porada, P., & Bader, M. Y. (2020). Interactions of epiphytes with precipitation partitioning. In J. T. Van Stan II, E. Gutmann, & J. Friesen (Eds.), *Precipitation partitioning by vegetation - A global synthesis*. Cham: Springer Nature.
- Mendieta-Leiva, G., & Zotz, G. (2015). A conceptual framework for the analysis of vascular epiphyte assemblages. *Perspectives in Plant Ecology Evolution and Systematics*, 17, 510–521. <https://doi.org/10.1016/j.ppees.2015.09.003>
- Moffett, M. W. (2000). What's "up"? A critical look at the basic terms of canopy biology. *Biotropica*, 32, 569–596. <https://doi.org/10.1111/j.1744-7429.2000.tb00506.x>
- Nadkarni, N. M., & Sumera, M. M. (2004). Old-growth forest canopy structure and its relationship to throughfall interception. *Forest Science*, 50, 290–298.
- Olson, D. M., Dinerstein, E., Wikramanayake, E. D., Burgess, N. D., Powell, G. V. N., Underwood, E. C., ... Kassem, K. R. (2001). Terrestrial ecoregions of the world: A new map of life on Earth. *BioScience*, 51, 933–938. [https://doi.org/10.1641/0006-3568\(2001\)051\[0933:-Teotwa\]2.0.Co;2](https://doi.org/10.1641/0006-3568(2001)051[0933:-Teotwa]2.0.Co;2)
- Parra, M. J., Acuña, K., Corcuera, L. J., & Saldaña, A. (2009). Vertical distribution of Hymenophyllaceae species among host tree microhabitats in a temperate rain forest in Southern Chile. *Journal of Vegetation Science*, 20, 588–595. <https://doi.org/10.1111/j.1654-1103.2009.01078.x>
- Petter, G., Wagner, K., Wanek, W., Delgado, E. J. S., Zotz, G., Cabral, J. S., & Kreft, H. (2016). Functional leaf traits of vascular epiphytes: Vertical trends within the forest, intra- and interspecific trait variability, and taxonomic signals. *Functional Ecology*, 30, 188–198. <https://doi.org/10.1111/1365-2435.12490>
- Ricklefs, R. E. (2008). *The economy of nature* (6th ed.). W. H. Freeman.
- Ruiz-Cordova, J. P., Toledo-Hernández, V. H., & Flores-Palacios, A. (2014). The effect of substrate abundance in the vertical stratification of bromeliad epiphytes in a tropical dry forest (Mexico). *Flora - Morphology, Distribution, Functional Ecology of Plants*, 209, 375–384. <https://doi.org/10.1016/j.flora.2014.06.003>
- Sanford, W. W. (1968). Distribution of epiphytic orchids in semi-deciduous tropical forest in Southern Nigeria. *Journal of Ecology*, 56, 697–705. <https://doi.org/10.2307/2258101>
- Sarmiento Cabral, J., Petter, G., Mendieta-Leiva, G., Wagner, K., Zotz, G., & Kreft, H. (2015). Branchfall as a demographic filter for epiphyte communities: Lessons from forest floor-based sampling. *PLoS ONE*, 10, e0128019. <https://doi.org/10.1371/journal.pone.0128019>
- Stuntz, S., Simon, U., & Zotz, G. (2002). Rainforest air-conditioning: The moderating influence of epiphytes on the microclimate in tropical tree crowns. *International Journal of Biometeorology*, 46, 53–59. <https://doi.org/10.1007/s00484-001-0117-8>
- Taylor, A., & Burns, K. (2015). Epiphyte community development throughout tree ontogeny: An island ontogeny framework. *Journal of Vegetation Science*, 26, 902–910. <https://doi.org/10.1111/jvs.12289>
- The Plant List (2013). *Published on the Internet*. <http://www.theplantlist.org/>
- Urrutia, R., & Vuille, M. (2009). Climate change projections for the tropical Andes using a regional climate model: Temperature and precipitation simulations for the end of the 21st century. *Journal of Geophysical Research-Atmospheres*, 114, <https://doi.org/10.1029/2008jd011021>
- Van der Werff, H., & Consiglio, T. (2004). Distribution and conservation significance of endemic species of flowering plants in Peru. *Biodiversity and Conservation*, 13, 1699–1713. <https://doi.org/10.1023/B:Bioc.0000029334.69717.F0>
- Wagner, K., Mendieta-Leiva, G., & Zotz, G. (2015). Host specificity in vascular epiphytes: A review of methodology, empirical evidence and potential mechanisms. *AoB Plants*, 7, plu092. <https://doi.org/10.1093/aobpla/plu092>
- Wagner, K., & Zotz, G. (2020). Including dynamics in the equation: Tree growth rates and host specificity of vascular epiphytes. *Journal of Ecology*. <https://doi.org/10.1111/1365-2745.13333>
- Wester, S., Mendieta-Leiva, G., Nauheimer, L., Wanek, W., Kreft, H., & Zotz, G. (2011). Physiological diversity and biogeography of vascular epiphytes at Río Changuinola, Panama. *Flora - Morphology, Distribution, Functional Ecology of Plants*, 206, 66–79. <https://doi.org/10.1016/j.flora.2010.01.011>
- Whittaker, R. H., Levin, S. A., & Root, R. B. (1975). Reasons for distinguishing niche, habitat, and ecotope. *American Naturalist*, 109, 479–482. <https://doi.org/10.1086/283018>
- Wickham, H. (2016). *ggplot2: Elegant Graphics for Data Analysis*. New York, NY: Springer-Verlag.
- Zotz, G. (2013a). 'Hemiepiphyte': A confusing term and its history. *Annals of Botany*, 111, 1015–1020. <https://doi.org/10.1093/aob/mct085>
- Zotz, G. (2013b). The systematic distribution of vascular epiphytes - a critical update. *Botanical Journal of the Linnean Society*, 171, 453–481. <https://doi.org/10.1111/boj.12010>
- Zotz, G. (2016). *Plants on plants - The biology of vascular epiphytes*. Switzerland: Springer.
- Zotz, G., & Bader, M. Y. (2011). Sampling vascular epiphyte diversity - species richness and community structure. *Ecotropica*, 17, 103–112.
- Zotz, G., Bogusch, W., Hietz, P., & Ketteler, N. (2010). Growth of epiphytic bromeliads in a changing world: The effects of CO₂, water



- and nutrient supply. *Acta Oecologica*, 36, 659–665. <https://doi.org/10.1016/j.actao.2010.10.003>
- Zotz, G., & Hietz, P. (2001). The physiological ecology of vascular epiphytes: Current knowledge, open questions. *Journal of Experimental Botany*, 52, 2067–2078.
- Zotz, G., & Vollrath, B. (2003). The epiphyte vegetation of the palm *Socratea exorrhiza* - correlations with tree size, tree age and bryophyte cover. *Journal of Tropical Ecology*, 19, 81–90. <https://doi.org/10.1017/s0266467403003092>
- Zuleta, D., Benavides, A. M., López-Rios, V., & Duque, A. (2016). Local and regional determinants of vascular epiphyte mortality in the Andean mountains of Colombia. *Journal of Ecology*, 104, 841–849. <https://doi.org/10.1111/1365-2745.12563>

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

Appendix S1. New header data specific for vascular epiphyte assemblage records in EpIG-DB 1.0 added to TurboVeg.

Appendix S2. List of databases detailing authors, project, funding source and references.

Appendix S3. Number of plots distributed across area size classes.

Appendix S4. Number of trees per diameter at breast height (DBH) and height class.

Appendix S5. Density of EPIG-DB datasets across the tropics and subtropics.

How to cite this article: Mendieta-Leiva G, Ramos FN, Elias JPC, et al. EpIG-DB: A database of vascular epiphyte assemblages in the Neotropics. *J Veg Sci.* 2020;00:1–11. <https://doi.org/10.1111/jvs.12867>